

The rhynchonellide brachiopod *Isopoma* Torley and its distribution

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SYNOPSIS. The Devonian rhynchonellid brachiopod genus *Isopoma* Torley, 1934, is described, with comments on species recorded from various geographic regions. *Isopoma maymyoensis* sp. nov. is erected for some specimens from the Late Eifelian to Early Givetian Padaukpin beds of Burma. *Isopoma* is mainly Eifelian to Givetian, Middle Devonian, in age. There are two species in the Pragian and Emsian, Lower Devonian, but possible occurrences in the Frasnian, Upper Devonian, have yet to be proved. Biogeographically the genus belongs to the Rhenish-Bohemian Region of the Old World Realm and has Rhenish affinities.

INTRODUCTION

Having discovered specimens of *Isopoma* Torley, 1934, incorrectly identified, we determined to investigate this poorly known genus to determine its stratigraphic and biogeographic distribution. One of us had previously identified the genus in north Spain (Mohanti, 1972) and, while investigating that fauna, studied specimens of *Isopoma* from various localities in Germany housed at the Senckenberg Natural History Museum at Frankfurt.

MATERIAL

We have studied specimens representing *Isopoma brachyptyctum* (Schnur), *I. gryps* Schmidt, *I. orthoglossa* (Torley), *I. ? ren* Schmidt, and *I. xestum* Torley from the Devonian of Germany, as indicated under the species descriptions. We have also studied specimens in the collections of the Natural History Museum, London, including specimens of *Rhynchonella? lummatoniensis* Davidson, 1865, which we assign to *Isopoma* and for which a lectotype is selected, and the collections from Burma figured and described by Anderson, Boucot & Johnson (1969). Some specimens in this collection identified as *Uncinulus subsignata* (Reed), are described here as *Isopoma maymyoensis* sp. nov. Mohanti also studied *Isopoma hertae* from the Cantabrian Mountains, Spain, housed in the National Natural History Museum, Leiden, Netherlands, which he had described in 1972. Our comments on other species of *Isopoma* are based largely upon information from the literature.

SYSTEMATIC DESCRIPTIONS

Most of the material described here is housed in the BMNH collections of The Natural History Museum, London, and these have registration numbers prefixed by B, BB, or BD. Register numbers of specimens in the Forschungsinstitut Senckenberg, Frankfurt, Germany, have the prefix SMF.

Order **RHYNCHONELLIDA** Kuhn, 1949
Superfamily **PUGNACOIDEA** Rzhonsnitskaya, 1956
Family **ASEPTIRHYNCHIIDAE** Savage, 1996

DIAGNOSIS. Pugnacoidea lacking dental plates, dorsal median septum or septalium; fold and sulcus developed anteriorly.

DISCUSSION. Savage (1996) introduced the family Aseptirhynchidae, which included *Aseptirhynchia* Soja, 1988. *Brunnirhynchia* Havlíček, 1979, *Carolirhynchia* Havlíček, 1992; *Chilimia* Baranov, 1978 and *Isopoma* Torley, 1934. Xu Han-kui and Yao Zhao-kui (1984: 561, table 3) described a new family, the Katuniidae, in which they placed *Isopoma* Torley, 1934. Savage (1996), in his major revision of Palaeozoic rhynchonellides, placed *Katunia* with weak dental plates in the Leiorhynchinae, while *Isopoma* was assigned to the new family, the Aseptirhynchidae, which lacks both dental plates and a dorsal median septum. Genera in the family are united by their similar external morphologies, i.e. their posterior smooth shells, and a tendency towards the anterior development of a fold and sulcus in which a few ribs developed. In some, weak additional ribs occur flanking the sulcus. The genera are differentiated principally on their internal characters. In two, *Chilimia* and *Aseptirhynchia*, dental plates are either weakly present or developed only in early ontogeny. Shell wall thickening is variable: in *Chilimia* the walls appear to be thin (Baranov, 1978: text–fig. 1); in *Aseptirhynchia* the ventral valve walls became thickened and overgrew the juvenile dental plates, but the dorsal valve remains relatively thin; in *Isopoma* both valves became thickened, but the hinge plates remain free, and the teeth and sockets are particularly strongly developed; in *Carolirhynchia* and *Brunnirhynchia* the valve wall thickening fused the hinge plates to the dorsal interior, leaving only a groove between the median edges. A further distinction in *Chilimia* is that the hinge plates only became medially disjunct at their anterior extremities.

DISTRIBUTION. *Aseptirhynchia* occurs in the Emsian of Alaska. *Carolirhynchia* was reported originally from Pragian and Emsian beds in the Barrandian area of Bohemia, although Savage (1996) reported the genus as restricted to the Eifelian. *Chilimia* is reported from the Middle Devonian of northeast Russia. *Isopoma* was originally described from the Middle Devonian of Germany, but is fully described below. *Brunnirhynchia* is of Early Famennian age from the Bruno area of the Czech Republic.

Genus *ISOPOMA* Torley, 1934

TYPE SPECIES. *Terebratula brachyptycta* Schnur 1853, by original designation.

DIAGNOSIS. Aseptirhynchid lacking adult dental plates, with dorsal valve thickening confined umbonally and free, disjunct hinge plates extending from well-developed inner socket ridges. Ventral valve thick-walled with prominent teeth. There are no median septa in either valve.

COMMENT. Below we describe or comment on the twelve species described as belonging to *Isopoma*, including one new species. The name *I. brachyptyctum* has been used in Germany to include specimens resembling the lectotype of Schmidt (1941), which are longer than wide, as well as more equidimensional specimens commonly found in the Middle and Upper Givetian strata, typically to the east of the river Rhine, Germany. We provide here some sections taken from both forms but have insufficient information to be able to differentiate these forms clearly, other than by their exteriors. Other species, eg. *I. orthoglossa* (Torley) and *I. ovale* Xian & Jian, somewhat resemble the wide forms of *I. brachyptyctum* and are of similar age. Further studies of these faunas are required to resolve these taxonomical problems and the stratigraphical range of true *I. brachyptyctum*.

SHELL STRUCTURE. The shell structure of *Isopoma* (Figs 19–21) is poorly known; no primary layer has been seen in fresh condition, but the secondary fibres are relatively large and angular; being somewhat rhomboidal in section. This is characteristic of many Palaeozoic rhyntonellids.

Isopoma brachyptyctum (Schnur, 1853) Figs 1–5, 19

1853 *Terebratula brachyptycta* Schnur: 178: pl. 23, fig. 6.

1934 *Isopoma brachyptyctum* (Schnur); Torley: 81, pl. 3, figs 12–15.



Figs 1, 2 *Isopoma brachyptyctum* (Schnur). 1, syntype; copy of Schnur, 1853: pl. 23, fig. 6; presumed from Eifelian limestone, Blankenheim, Germany; Schnur Collection, Geol.-Paläontological Institute, Bonn; $\times 2$. 2, lectotype; a syntype from the Schnur Collection resembling that of Fig. 1; copy of Schmidt 1941: pl. 4, fig. 88; locality unspecified, but possibly Ahrdorf Formation, Eifelian, Germany; $\times 2$. Both specimens are illustrated in dorsal, anterior and ventral views, but note that Schmidt illustrated the anterior view with the ventral valve uppermost.

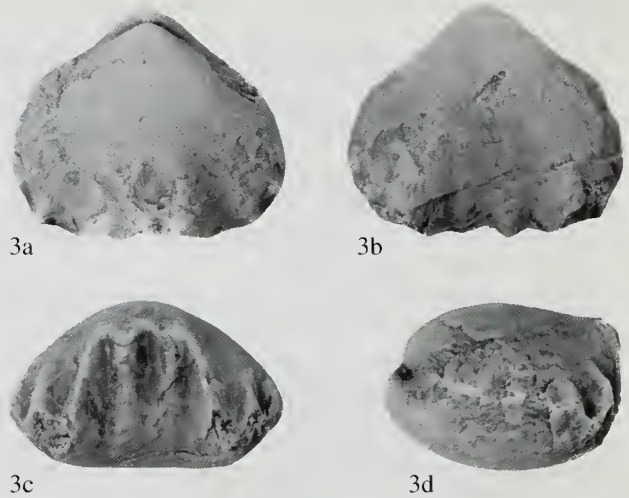


Fig. 3 *Isopoma brachyptyctum* (Schnur). Dorsal, ventral, anterior and lateral views; Givetian Massenkalk, Bilveringsen, Germany; BD 12784, $\times 3$.

1941 *Isopoma brachyptyctum* (Schnur); Schmidt: 45, pl. 4, fig. 88.

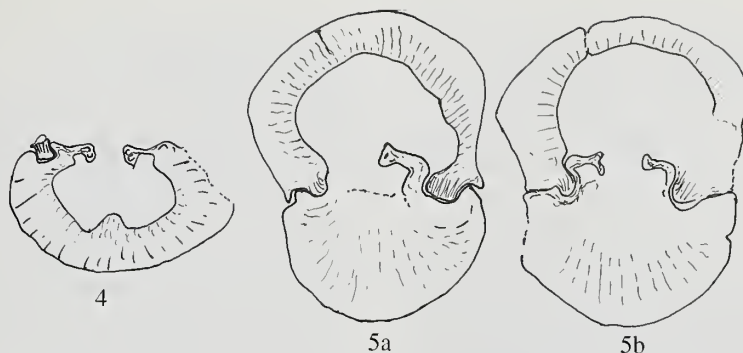
1966 *Isopoma brachyptyctum* (Schnur); Biernat: 106, pl. 22, figs 1–9.

TYPE SPECIMEN. The lectotype, selected by Schmidt (1941: 45, pl. 4, fig. 88), is from Im Kalk zu Blankenheim (Schnur, 1853: 178). Schmidt did not specify the precise stratigraphical level of this specimen, which is in the Schnur Collection at the Geol.-Paläontological Institute, Bonn, Germany. However, the lectotype possibly came from the Ahrdorf Formation (Mohanti, 1972: 170), which is considered to be Middle Eifelian in age (see Paulus, Struve & Wolfart, 1963: 466, text-fig. 1).

DIAGNOSIS. Outline approximately equidimensional, with greatest width at about two-thirds of the length of the shell; ventral sulcation prominent, commonly containing two ribs and an additional pair of ribs lateral to the sulcus; fold weakly developed.

MATERIAL. German specimens from the Eifel region are: 3 specimens (SMF XVII 342b, XVII 342c and XVII Bi) from Bilveringsen; one specimen (SMF XVII 1168a) from Schleddenhof; one specimen (SMF XVII 342k) from the Ahrdorf Formation at Gees; and 5 specimens (SMF XVII 2420) from the Ahabach Formation at Hallert. In addition, unregistered specimens were kindly donated by the late Dr Struve from the upper part of the Lahr Member of the Ahabach Formation (Loc. St. 949) (BD12782–83) and from the Massenkalk (Kohlenstein Member) of the Kohlenstein quarry at Iserlohn-Bilveringsen (BD 12784).

STRATIGRAPHICAL RANGE. According to Schmidt (1941: 45), in the Eifel area of Germany *Isopoma brachyptyctum* ranges from Middle Eifelian (Ahrdorf Formation) to the Fleringen Schichten, which is now known to range from the Ahabach Formation (uppermost Eifelian) to the Curten Formation (Lower Givetian) (Paulus, Struve & Wolfart, 1963: 466, text-fig. 1). The species is also known to the east of the Rhine river in Germany. Torley (1934) described *Isopoma brachyptyctum* (Schnur) from the Massenkalk (Upper Givetian) of Bilveringsen, near Iserlohn. Schmidt (1951) also briefly remarked upon a specimen of *Isopoma brachyptyctum* from the Upper Givetian Flinz kalk of Schleddenhof, near Iserlohn-Letmathe on the east side of the Rhine.



Figs 4, 5 *Isopoma brachyptyctum* (Schnur). **4**, section of a dorsal valve at the socket showing well defined, separated, outer hinge plates and crural bases; Ahbach Formation, Lahr Member, mid-Eifelian, Im Lahr, NE of Niederehe, St. 949, Germany; BD 12782, $\times 9$. **5a, b**, sections through a shell near the socket, where the valve is thickened, slightly posterior and dorsal to that of Fig. 4; Massenkalk, Kohlenstein Member, Upper Givetian, Iserlohn-Bilvergsen, Germany; BD 12783, $\times 9$.

Maillieux (1941: 10) listed *Isopoma aptyctum* (Schnur) and *I. brachyptyctum* from Frasnien (F₂ beds) in the Devonian of Ardenne, Belgium, but gave no description or illustrations, so the validity of these occurrences cannot be verified.

Havlíček (1951, 1961) reported *I. brachyptyctum* (Schnur) from the Middle Devonian (Givetian) limestones in the vicinity of Čelechovice (Moravia). Biernat (1966) described specimens of *I. brachyptyctum* (Schnur) from the Skaly Beds and one from the Pokrzywianka beds, Holy Cross Mountains, Poland. Although there is some difficulty about the Eifelian/Givetian age for the Skaly Beds, Biernat (1966) thought them to be Lower Givetian on the basis of her brachiopod study.

Bublikhenko (1974: 72, 73, pl. 10, figs 8–10) described and illustrated *I. brachyptyctum* (Schnur) from the Krjukovo Beds (Lower? Emsian) of the Russian Rudnogo Altai region. However, serial sections and precise information about the interior is lacking, so the identification is doubtful.

Sapel'nikov & Mizens (1984: 23–24, pl. 4, figs 10, 13, pl. 5, figs 4, 5) described and figured *I. aff. brachyptyctum* (Schnur) from beds with *Ivdelinia acutolobata* of Lower Givetian age from the central part of the Ufa Amphitheatre in the southwest Urals, Russia. Mamedov (1985) reported the occurrence of *Isopoma brachyptyctum* in a key section of the Middle Devonian of Transcaucasia, in the upper Arpachaisk sub-suite of Givetian age. He claimed that this interval corresponds with the Alchedatskii horizon of the Kuznetsk Basin, the upper parts of the Starooskolskii (old Oskolskii) horizon (Mulinskii/Moulins beds) on the Russian platform and possibly the upper parts of the Aidarlinskii horizon of Kazakhstan. According to Mamedov (1985: 159) the Mont-Aur Layers with *Hexagonaria quadrigemina* in the Ardennes correspond to this interval and the Boldsdorf layers in the Eifel are possibly synchronous.

Sapel'nikov & Mizens (1985), while providing new data on the biostratigraphy of the Ural Mountains, recorded *Isopoma aff. brachyptyctum* on both western and eastern slopes, at a stratigraphic level which they correlated with the Eifelian-Givetian horizons of the Ardennes-Rhine region of Western Europe.

Xian Si-yan & Jiang Zong-long (1978: 289, pl. 106, fig. 14) described and illustrated *I. brachyptyctum* (Schnur) from the lower part of the Dushan Formation (Givetian), Dongyao, Xiasi, Dushan County, Guizhou, China. Although no internal information was given, the shape resembles that of the lectotype figured by Schmidt (1941: 45, pl. 4, fig. 88). Xian & Jiang (1978) did not give detailed

information on the stratigraphic levels from which their two species (*I. brachyptyctum* and *I. ovale*) were found.

Isopoma alecto (Barrande, 1847)

1847 *Terebratula alecto* Barrande: 42, pl. 20, fig. 2.

1961 *Isopoma alecto* (Barrande); Havlíček: 40, pl. 6, fig. 5.

COMMENT. This species was described from the Pragian of Bohemia. Havlíček's (1961) redescription showed that it is characterized by a ventral sulcus starting just before half the valve length and containing three ribs. Havlíček (1961: 40, text-fig. 7) also gave a section showing a thin divided hinge plate and crural bases, which are directed dorsally, as in all known *Isopoma* species. Havlíček (1992: 56, table 1) listed this species in the Suchomasty Limestones (Dalejan). The species name was used by Perry (1984) for specimens from the Upper Lochkovian of the Yukon Territory in Arctic Canada. However, we think more critical studies are necessary before accepting the Yukon forms as true *Isopoma*.

Isopoma gryps Schmidt, 1965

Fig. 6

1965 *Isopoma gryps* Schmidt: 13–16, text-figs 18, 19; pl. 1, figs 1–7.

MATERIAL. From Greifenstein, Eifel region, Germany, 17 specimens (SMF 19531) and two unregistered specimens, donated by the late Dr Struve, from an exploration trench from the Greifensteinkalk of the same area (BD 12786–87).

COMMENT. This species was originally described from the Lower Eifelian Greifensteiner Kalk of the Eifel region. It is characterized by a prominent ventral sulcus, which originates close to the umbo. In some specimens the sulcus contains a single median rib. Serial sections (Fig. 6a–c) show characters typical of the genus, with a thickened dorsal umbo and prominent teeth.

Isopoma hertae Mohanti, 1972

Figs 7, 8

1972 *Isopoma hertae* Mohanti: 170, pl. 6, fig. 4, pl. 7, figs 1–5.

COMMENT. Specimens were originally described from the upper Eifelian to Givetian transitional beds in the Cantabrian Mountains, northern Spain, and these have been studied. This species is characterized by a circular to subpentagonal outline, weakly developed

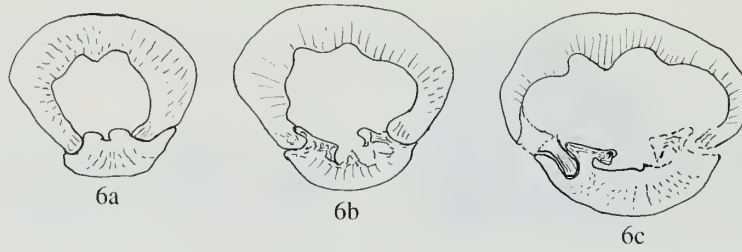


Fig. 6 *Isopoma gryps* Schmidt. Sections through the socket region of a poorly preserved specimen showing thickened valves. Greifenstein Kalk, Lower Eifelian, trench at Wiege, Greifenstein, Hessen, Germany; BD 12786, $\times 9$.

uniplication modified by a zig-zag commissure resulting from 6–7 short, anteriorly confined ribs. The ventral valve is further ornamented by a median groove originating close to the umbo.

Isopoma hertae has also been recorded by Fícnér & Havlíček (1978) from the Lower Givetian beds of the Čelechovice area in Moravia, Czech Republic.

Isopoma isiliense Rzhonsnitskaya, 1953

1953 *Isopoma isiliensis* Rzhonsnitskaya: 177, pl. 10, figs 12, 13.

COMMENT. The only known occurrence is the original description of specimens from the Upper Frasnian of the Kuznetsk Basin,



Fig. 7 *Isopoma hertae* Mohanti. Dorsal, ventral, anterior and lateral (anterior uppermost) views; Portilla Formation (Eifelian to Givetian) of southern Cantabrica, Spain; BD12734, $\times 3$.

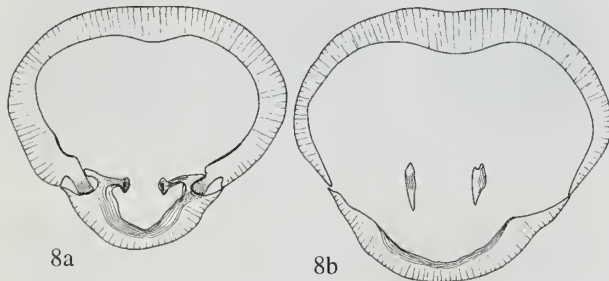
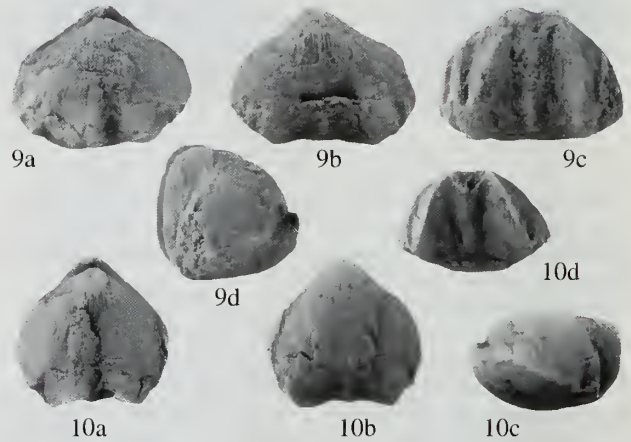


Fig. 8 *Isopoma hertae* Mohanti. Portilla Formation (Eifelian to Givetian), Cantabrica, Spain; sections of the specimen figured by Mohanti (1972: figs 30.2, 30.3); specimen not registered, Geologisch en Mineralogisch Instituut, Rijksuniversiteit, Leiden, $\times 8$.



Figs 9, 10 *Isopoma lummatoniensis* (Davidson). 9a–d, *Lectotype*, here selected (figured Davidson, 1865: pl. I4, fig. 14); dorsal, ventral, anterior and lateral views with the umbo to the right; late Givetian, Lummaton, Devon; BB 61841, $\times 3$. 10a–d, dorsal, ventral, anterior and lateral views (with the umbo to the left); late Givetian, Lummaton, Devon; B 12802, $\times 3$.

Russia (Rzhonsnitskaya, 1953). The species is poorly characterized, but appears to be rather small and deep bodied, with 3 ribs in the ventral sulcus. Interiors are unknown.

Isopoma lummatoniensis (Davidson, 1865) Figs 9–11, 21

1865 *Rhynchonella lummatoniensis* Davidson: 70, pl. 14, figs 14–17.

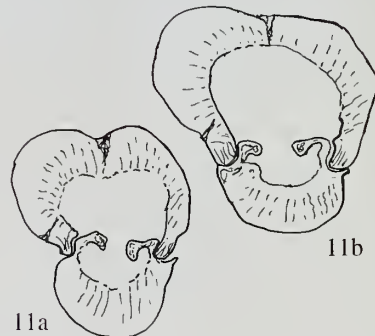


Fig. 11 *Isopoma lummatoniensis* (Davidson). Sections through the socket and hinge plate region. Lummaton Shell Bed, late Givetian, Lummaton, Devon; BB 51959, $\times 9$.

?1953 *Isopoma lummatoniensis* (Davidson); Rzhonsnitskya: 176, pl. 10, figs 14, 15.

TYPE SPECIMEN. BB 6184, figured by Davidson (1865: pl. 14, fig. 14), is here selected lectotype (Fig. 9a–d).

COMMENT. Davidson (1865), described a series of quarries at Lummaton, about 3 miles north of Torquay, Devon. He referred to the beds as the Stringocephalus Burtini Beds. The Lummaton Shell Bed is part of this series of late Givetian fossiliferous limestones. Davidson (1882: 11) said Rigaux (1878) had recorded *Rhynchonella lummatoniensis* at Ferques, France. However, the extensive ecological study by Wallace (1966; 1969) in that area did not record the species, so we are doubtful about *Isopoma* occurring at Ferques.

The species is characterized by its high ventral sulcus containing a single rib and the deep body cavity; the dorsal valve has a corresponding long narrow median groove. Davidson (1865: pl. 14, fig. 15) figured a second syntype of *Rhynchonella lummatoniensis* which is less deep-bodied and has two ribs in the ventral sulcus. This might be conspecific with the lectotype, but it recalls the similarly shallow specimen of *I. maymyoensis* described below. Large collections might reveal whether these shallower specimens with more ribs are really conspecific.

Rzhonsnitskya (1953: 176, pl. 10, figs 14, 15) recorded and illustrated *I. lummatoniensis* from the Frasnian of the Kuznetsk Basin, Russia, but internal structures of these specimens are very poorly known and generic assignment remains in doubt.

Isopoma maymyoensis sp. nov.

Figs 12–14, 20

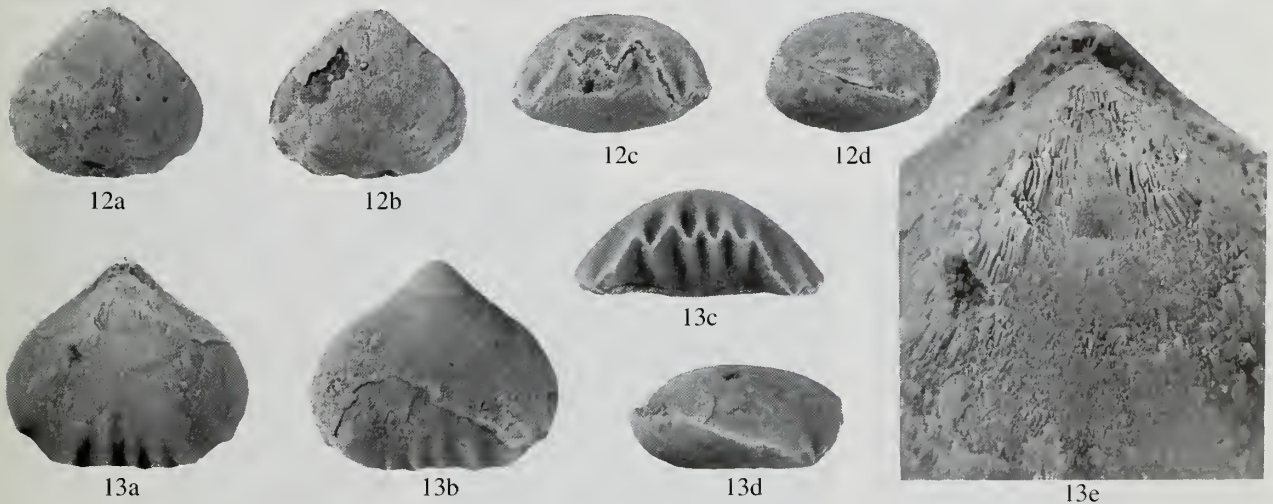
1969 *Uncinulus subsignata* Reed; Anderson *et al.*: 137, pl. 5, figs 18–21 (non figs 22–31).

ETYMOLOGY. The species is named from Maymyo, Burma, the region from which the material was collected.

TYPE SPECIMEN. The holotype (BB 55546; figured Anderson, Boucot & Johnson, 1969: pl. 5, figs 18, 19) is from the Padaukpin Limestone (late Eifelian to early Givetian), Padaukpin, 10 miles NE of Maymyo, Central Burma.

DIAGNOSIS. *Isopoma* with relatively shallow body cavity and weakly developed uniplication modified by 1–3 short ribs within the sulcus; an additional pair of ribs may occur laterally; hinge plates well separated both medially and from the dorsal valve floor.

COMMENT. Anderson *et al.*'s (1969) description of *Uncinulus subsignata* included smaller specimens which are here called *Isopoma maymyoensis*, as well as larger specimens (Anderson *et al.*, 1969: pl. 5, figs 22–31) which we accept as *Nalivkinaria subsignata* (see Mohanti, 1972: 166). The age of the *Isopoma* specimens, together with *Nalivkinaria*, was originally given as probably Eifelian, but we extend the age of the beds into the Early Givetian (Mohanti & Brunton, 1992: 11). Ecologically *Isopoma maymyoensis* thrived in a shallow marine subtidal benthic level-bottom environment and the associated carbonates contain a variety of shelly fossils.



Figs 12, 13 *Isopoma maymyoensis* sp. nov., late Eifelian to lower Givetian, Padaukpin Limestone, Padaukpin, Burma. 12a–d, Holotype; dorsal, ventral, anterior and lateral views (note that the umbo is broken); BB 55546, $\times 4$. 13a–d, dorsal, ventral, anterior and lateral views, $\times 4$; 13e, detail of part of the dorsal valve, BB 55547, $\times 10$.

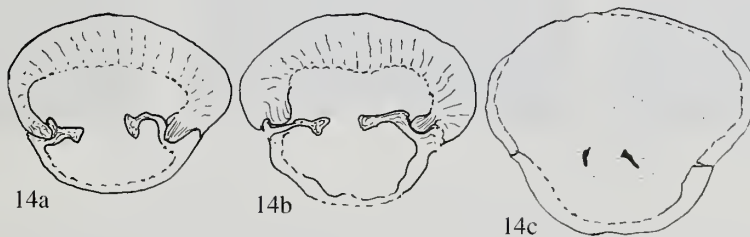


Fig. 14 *Isopoma maymyoensis* sp. nov. Sections at the sockets and hinge plates and anteriorly through the crura. Padaukpin Limestone, Burma, BB 55547, $\times 9$.



Fig. 15 *Isopoma orthoglossa* (Torley). *Lectotype*; dorsal, ventral, anterior and lateral views (with ventral valve uppermost); Flinzkalk, Givetian, Iserlohn, SMF XVII 1164a, $\times 2.5$ (from Schmidt, 1951: pl. 1, fig. 6).

***Isopoma nekhoroshevi* Bublichenko, 1974**

1974 *Isopoma nekhoroshevi* Bublichenko: 73, text-fig. 9; pl. 2, fig. 9.

COMMENT. This species is from the Emsian of the Rudnogo Altai, Ural Mountains, Russia. The specimens are small, the ventral sulcus starts near the ventral umbo and ribbing is confined anteriorly, associated with the fold and sulcus. The hinge plate appears to be divided (Bublichenko, 1974: text-fig. 9) and the lack of a median septum is normal for the genus.

***Isopoma orthoglossa* (Torley, 1908)**

Fig 15

1908 *Camarophoria orthoglossa* Torley: 29, pl. 3, figs 20, 21, pl. 4, figs 1-3.

1951 *Isopoma orthoglossa* (Torley); Schmidt: 87, pl. 1, figs 6a-d.

COMMENT. Schmidt (1951) redescribed this species from the Flinzkalk (Upper Givetian) in the Iserlohn-Letmathe area on the east side of the river Rhine, Germany. The lectotype (Schmidt, 1951: pl. 1, fig. 6) is comparable to the wide Givetian specimens of *Isopoma brachyptyctum*. No information on internal structures was given by Schmidt. Further work on this species and the wider form of *I. brachyptyctum* from the Upper Givetian of the eastern Rhine area is needed to establish their relationships. We have studied two specimens from Bilveringsen (SMF XVII 478a), but have not been able to prepare sections.

***Isopoma ovale* Xian Si-yan & Jiang Zong-long, 1978**

1978 *Isopoma ovale* Xian & Jiang: 289, pl. 106, fig. 13.

COMMENT. *Isopoma ovale* is from the lower part of the Dushan Formation (Givetian), Dongyao, Xiasi, Dushan County, Guizhou, China. Externally this species somewhat resembles the wider forms of *I. brachyptyctum* found in the Upper Givetian strata of Germany. Xian & Jiang (1978: 289) record 'dental plates fused with the wall of shell'. However, we have seen no evidence of dental plates as compared to simple shell wall thickening. They also report that crural plates and hinge plates are separated and the cardinal process absent. *I. ovale* differs from the type species in being wider in outline, having a weak sulcus and 7 to 8 anterior ribs close to the commissure.

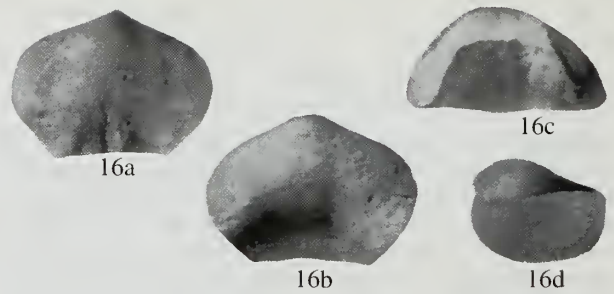


Fig. 16 *Isopoma? ren* Schmidt. *Holotype*, dorsal, ventral, anterior ($\times 2$) and lateral views; Flinzkalk, Schleddenhof bei Iserlohn; SMF XVII 1163a, $\times 1.7$ (from Schmidt, 1951: pl. 1).

***Isopoma? ren* Schmidt, 1951**

Fig. 16

?1908 *Camarophoria aptycta* (Schnur); Torley: 30, pl. 6, figs 4, 5.
1951 *Isopoma? ren* Schmidt: 88, pl. 1, fig. 4.

COMMENT. Schmidt assigned her species doubtfully to *Isopoma*; it is from the Upper Givetian Flinzkalk in the Iserlohn-Letmathe area, Germany. The figured specimen (Schmidt, 1951: pl. 1, fig. 4) appears to be somewhat wider than *I. brachyptyctum*, deeper bodied and has indistinct ribs. Schmidt described a divided hinge plate, weakly curved and ventrally directed crura, and the absence of an internal median septum, all features that are consistent with *Isopoma*. We have seen two specimens from Schleddenhof (SMF XVII 1163b, 1163c), but have not been able to prepare sections for internal study.

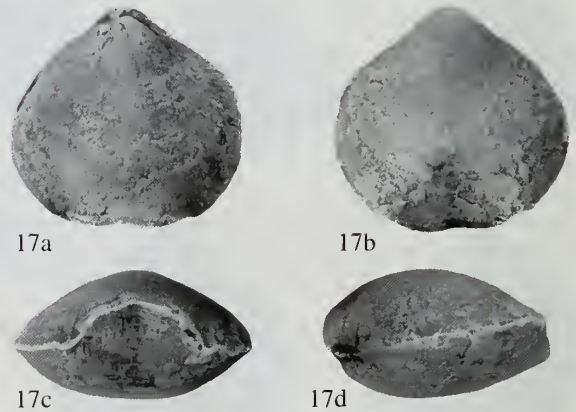


Fig. 17 *Isopoma xestum* Torley. Dorsal, ventral, anterior and lateral views; Givetian, Massenkalk, Bilveringsen, Germany; BD 12785, $\times 3$.

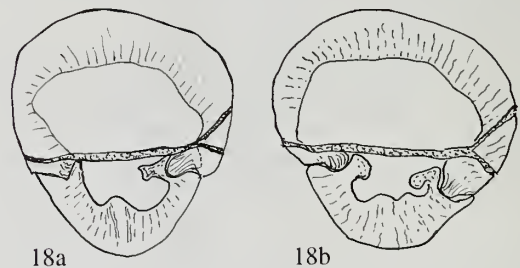


Fig. 18 *Isopoma xestum* Torley. Sections through the specimen from Massenkalk, Germany, figured in Fig. 17, $\times 9$.

Isopoma xestum Torley, 1934

Figs 17, 18

1934 *Isopoma xestum* Torley: 82, pl. 3, figs 16, 17.

COMMENT. This species is from the Upper Givetian Massenkalk of Bilveringsen near Iserlohn on the east of the Rhine, Germany. The figured specimens are small and less deep than typical *I. brachyptyctum* and do not show ribbing. We have studied 11 specimens (SMF XVII 347c) and an unregistered specimen, donated by the late Dr Struve, from the Kohlenstein member of the Massenkalk at the Kohlenstein quarry in the Iserlohn Bilveringsen area (BD 12785). The sectioned specimen is not well preserved so the internal features remain poorly known and reference of the species to *Isopoma* remains insecure.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION OF *ISOPOMA*

Twelve species of *Isopoma* are described or commented upon above; *I. aptyctum* (Schnur), of supposed Frasnian age, is very poorly known, and we have not been able to study specimens, so we do not describe it here. Of these twelve reasonably established species, eight are from the Eifelian to Givetian of the Middle Devonian, and two (*I. alecto* (Barrande) and *I. nekhoroshevi* Bublichenko) from the Pragian and Emsian of the Lower Devonian are doubtfully referred to *Isopoma*. Two more species (*I.?* *ren* Schmidt and *I. xestum* Torley), from the upper Givetian might belong to *Isopoma*, but they are also poorly known. We, therefore, suggest a well established stratigraphical range for *Isopoma* in the Eifelian and Givetian, with less securely established species in later Lower Devonian rocks.

Isopoma appears to be absent from the Devonian of Morocco (Drot, 1964) and Afghanistan (Durkoop, Mensink & Plodowski, 1967; Durkoop, 1970). Brice (1971), however, described specimens from Afghanistan as *Kransia?* cf. *subsignata* (Reed, 1908), and

suggested they are conspecific with specimens from Burma figured by Anderson, Boucot & Johnson (1969) as *Uncinulus subsignata* (Reed). We do not think Brice's (1971) illustrations belong to what would now be called *Nalivkinaria subsignata*, or to either *Beckmannia* or *Isopoma*.

The palaeogeographical map (Fig. 22) shows the distributions of *Isopoma* species.

PALAEOBIOGEOGRAPHY

Devonian brachiopod biogeography has been discussed in detail by Boucot (1988). *Isopoma* is typically a Middle Devonian brachiopod belonging to the Rhenish-Bohemian Region of the Old World Realm (Boucot, 1984) and has Rhenish provincial affinities (Struve, 1982a). The largely warm, shallow marine environment of this biogeographic region probably had complex current circulation patterns. Apart from palaeogeography, sea-level changes and the development of reefs and banks, the shallow seas and patterns of marine circulation might have influenced the variable faunal associations of the Middle Devonian of the Rhenish-Bohemian Region. Information on the Rhenish-Bohemian Region brachiopods shows them as occurring in parts of Europe, North Africa and Asia. The Lower and Middle Devonian faunas of most of north Africa are of Rhenish-Bohemian Region type (Boucot *et al.*, 1983). The Jauf Formation of Lower Devonian (Pragian-Emsian) age of northwestern Saudi Arabia contains brachiopods and trilobites which also belong to the Rhenish-Bohemian Region of the Old World Realm (Boucot, 1984; Boucot *et al.*, 1989).

A Rhenish type of Eifelian brachiopod fauna occurs in Armenia and the Tien Shan (Boucot *et al.*, 1988: 365). The biostratigraphy and biogeography of Devonian brachiopods in China have been described by Hou Hong-Fei (1981) and Wang Yu *et al.* (1984). The South China Province includes the south Tien Shan Mountains,



19



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Figs 19–21 Scanning electron micrographs of abraded valve exteriors illustrating macro-shell structures in three species of *Isopoma*. 19, *I. brachyptyctum* (Schnur), Eifel, Germany; same specimen as Fig. 3; ventral valve anterolateral flank, BD 12784, $\times 100$; 20, *I. maymyoensis* sp. nov., Burma; ventral valve (see Fig. 13), posterior to median sulcus, BB 55547, $\times 50$; 21, *I. lummatoniensis* (Davidson); Devon, England; ventral valve, posterolateral flank, BB12802, $\times 40$.

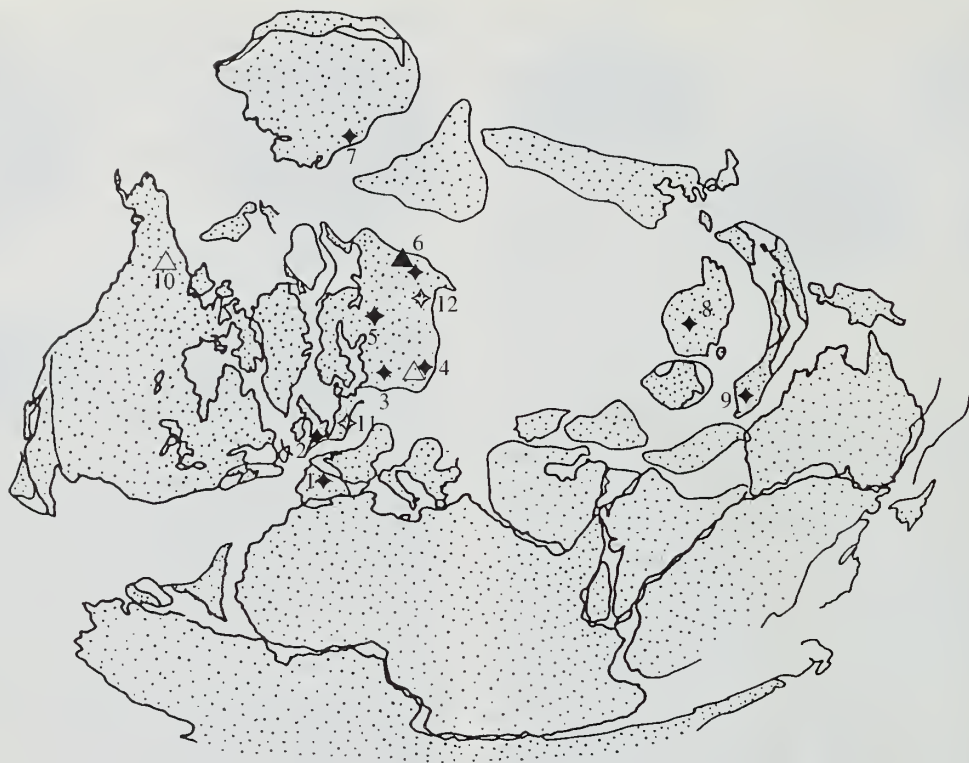


Fig. 22 World palaeogeographical map of the Middle Devonian (from Scotese & McKerrow, 1990) showing the distribution of *Isopoma* species. Δ – Lower Devonian, Pragian; \blacktriangle – Lower Devonian, Emsian; \blacklozenge – Middle Devonian, Eifelian to Givetian; \diamond – Upper Devonian, Frasnian. 1 – north Spain (*I. hertae*); 2 – Devon, England (*I. lummatoniensis*); 3 – Eifel, Germany (*I. brachyptyctum*, *gryps*, *orthoglossa*, *ren*, *xestum*); 4 – Czech Republic (*I. brachyptyctum*, *hertae*, and in Pragian, *I. alecto*); 5 – Poland (*I. brachyptyctum*); 6 – west Urals (*I. brachyptyctum* and in Emsian, *I. nekhoroshevi*); 7 – east Urals (*I. brachyptyctum*); 8 – Guizhou, China (*I. brachyptyctum. ovale*); 9 – Burma (*I. maymyoensis*); 10 – Yukon (*I. alecto*); 11 – Ardennes (*I. aptyctum*); 12 – Kuznetsk, Russia (*I. isiliensis*, ?*I. lummatoniensis*).

which are on the eastward extension of the Ural-Tien Shan marine belt, and brachiopods here are similar to those in Europe, including the Urals. During the early part of the Middle Devonian, three facies-related assemblages of brachiopods existed, reflecting different palaeoecological conditions. *Isopoma* is associated with the *Zdimir* community (Hou Hong-Fei, 1981) and restricted to limestone facies bordering platform areas. The facies is characterized by reefal limestones and biostromes composed of corals and stromatoporoids, together with abundant accumulations of *Zdimir* shells and occasional occurrences of other brachiopod genera. Farther to the north, in western Nei Monggol (Inner Mongolia), Eifelian brachiopods of the Rhenish-Bohemian Region, as well as taxa with Uralian affinities, have been described by Zhang Yan (1985; 1986). This indicates a biogeographic boundary transition comparable to that observed by Nalivikin (in Boucot *et al.*, 1988: 365) from the western Tien Shan. *Camaroforia lummatoniensis*, as recorded by Anderson *et al.* (1969: 118) from the Eifelian of western Yunnan, may belong to *Isopoma*. Adjacent to western Yunnan, Eifelian brachiopods with Rhenish affinities have also been described from the northern Shan State of Burma (Anderson *et al.*, 1969). These Middle Devonian (Eifelian to Lower Givetian) shelly faunas of Padaukpin are strikingly similar to those of the Eifel region of Germany and were first described from Burma by Reed (1908). The brachiopod fauna from the Padaukpin beds can be compared to the Middle Devonian Rhenish brachiopod faunas of the European Eifel region, Germany, the southern Cantabrian

Mountains, Spain, and the Holy Cross Mountains, Poland. The presence of *Beckmannia* and *Isopoma* in the Padaukpin brachiopod assemblage adds further evidence for the European Rhenish affinities of this brachiopod fauna as an eastern extension of the Rhenish-Bohemian Region of the Old World Realm. In view of the global high level of provincialism during the Eifelian, the similarity of the Middle Devonian shelly faunas of Padaukpin, Burma, to those of the distant Eifel region in Germany seems to be a biogeographic anomaly (Boucot *et al.*, 1988), as was also emphasized by Struve (1982b).

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